A. K. PANDEY*: **Developmental anatomy of seeds and fruits in *Galinsoga parviflora* and *Dahlia pinnata* (Asteraceae)**

A. K. パンデイ*: コゴメギクとダリアの種子と果実の形成

Genera *Galinsoga* (14 species) and *Dahlia* (28 species) are distributed in New World and Mexico to Colombia (Mabberley 1987). A perusal of literature reveals that development and structure of seeds and fruits in these taxa have not been investigated, hence this work was undertaken with the following specific objectives; 1) to describe the developmental anatomy of seed and fruit which have not been investigated so far, 2) to comment on the systematic significance of anatomical features of seed coat and pericarp, and 3) to trace the mode of deposition of phytomelanin in the achenes.

Material and methods Flowers and achenes of *Galinsoga parviflora* Cav. were collected from Dehra Dun (Pandey 4213) and those of *Dahlia pinnata* Cav. from the plants growing in Botanical Garden of Bhagalpur University (Pandey 3791). FAA fixed materials were stored in 70% ethanol. Customary methods of dehydration in TBA series and embedding in paraffin were followed. Microtome sections cut at 7–12 μm thickness were stained with safranin-fastgreen combination.

Observations

1) *Galinsoga parviflora*. Ovary and ovule. The syncarpous and unilocular ovary contains a single anatropous, unitegmic and tenuinucellate ovule (Fig. 1A, B). The ovule at the functional megaspore stage completely fills the ovarian chamber (Fig. 1A). The ovary grows fast, and at the organized female gametophyte stage the ovule occupies only 3/4 part of the locule (Fig. 1B), but as the seed matures, it again fills the entire space of the ovary chamber (Fig. 1I). The vascular supply of the ovule enters the funicle and passes through the chalaza ending on the antiraphe side up to about half the height of the integument (Fig. 1B).

Integument. The integument at the functional megaspore stage consists of 8–10 layers of parenchymatous cells (Fig. 1D). The innermost layer of the

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integument by this time has differentiated into a distinct endothelium and the nucellus is seen as a very thin layer around the megaspore.

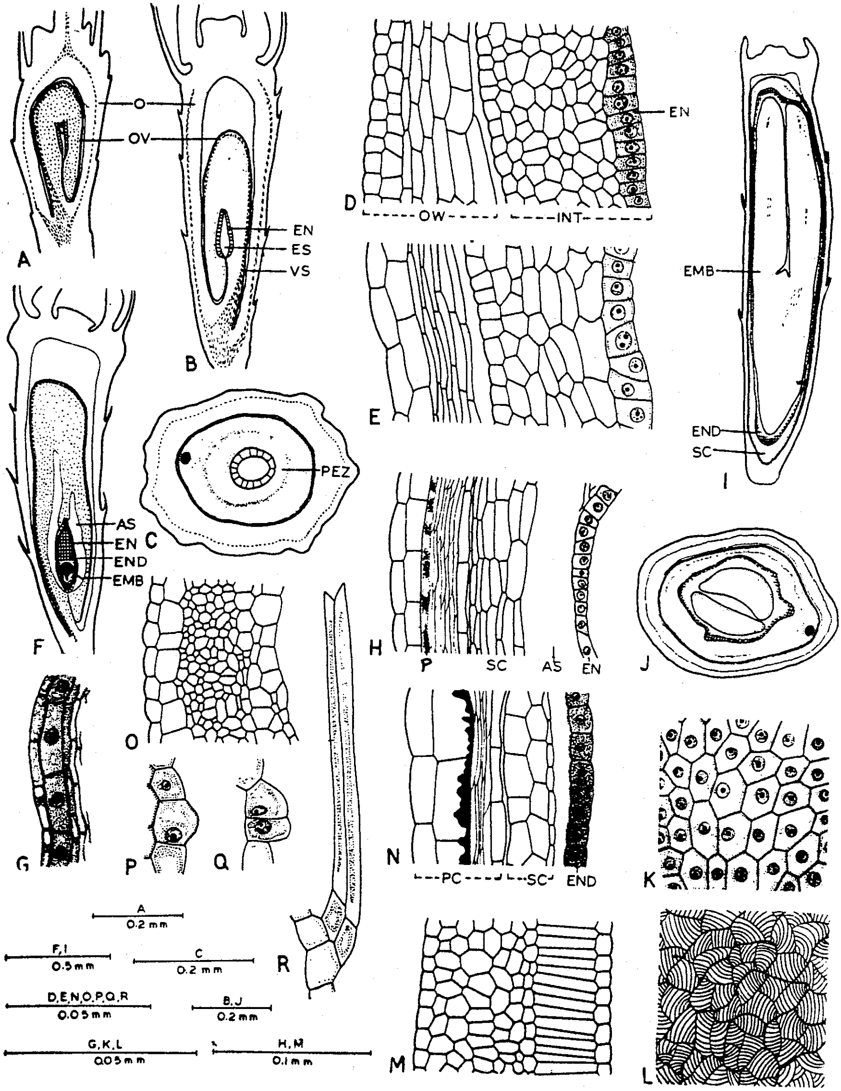
By the time female gametophyte is fully organized, the nucellus is fully consumed and the embryo sac comes in direct contact with the endothelium. Cells of a few layers of the integument around the endothelium enlarge considerably, become highly vacuolated and form the periendothelial zone (Fig. 1C, E). The integument at this stage is distinguishable into three distinct zones. The outer zone comprises cells having dense cytoplasm. The middle zone is the periendothelial region, and the inner zone is made up of a layer of endothelium. The outer epidermal cells of the integument, in surface view, show polygonal outline (Fig. 1K).

Endosperm and embryo. At the globular embryo stage, the endosperm cells completely fills the embryo sac (Fig. 1F). Quick digestion of endosperm begins at about the heart-shaped embryo stage and concomitantly, the cells of the outermost layer of the endosperm differentiate as a prominent layer by accumulating dense cytoplasm (Fig. 1G). In a mature seed, only one or two layers of the endosperm are left on the sides but the number is more on the radicular and cotyledonary ends (Fig. 1I).

The mature embryo occupies more or less the entire space in the seed (Fig. 1I). In a mature capitulum, the peripheral fruits show a little curved embryos while the centrally placed fruits have straight embryos. The hypocotyl-root-axis is slightly shorter than the cotyledons. The shoot apex is dome-shaped and is undifferentiated. The subepidermal cells of the cotyledons on the ventral side show radially elongated palisade cells (Fig. 1M). Rests of the cells are polygonal in outline and do not show any special feature. All the cells of the embryo contain reserve food material. Average length of embryo and its parts is given in Tab. 1.

Tab. 1. Size of cypsela, length of embryo, hypocotyl-root-axis and cotyledons (measurements in mm).

Species	Cypsela (l.×b.)	Embryo	Hypocotyl-root-axis	Cotyledons
Galinsoga parviflora	2×0.75	1.40	0.70	0.70
Dahlia pinnata	11×3.25	8.42	2.36	6.06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F, I
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C
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D, E, N, O, P, Q, R
0.05 mm
B, J
0.2 mm
G, K, L
0.05 mm
H, M
0.1 mm

Seed coat. After fertilization, the cells of the periendothelial zone begin to disorganize and by the time advanced globular embryo stage is reached, an air space appears in this region (Fig. 1F). The disorganization of the cells also extends towards the chalaza. The endothelium remains one layer thick throughout the length of the embryo sac except at a few places towards the chalazal side where a few cells divide periclinally. The tangential stretching of the endothelial cells starts at the late globular embryo stage and by the time two cotyledons are well differentiated, the endothelium is much stretched. Further disorganization of the integumentary cells results into a wide space around the embryo sac.

In a mature seed, the seed coat is 2-3 layers thick (Fig. 1N) except at the radicular and chalazal ends where the number is more. The endothelium by this time is fully consumed and persists as a thin noncellular pellicle over the outermost layer of the endosperm (Fig. 1N). The epidermal cells of the seed coat become irregular in outline and show characteristic fibrous thickenings (Fig. 1L).

Ovary wall and pericarp. Ovary wall at the functional megaspore stage is 7-9 layers thick at the level of the nucellus (Fig. 1D). Single layered epidermis is followed by a layer of hypodermis and these two layers are made up of smaller cells. Rests of the cells of the ovary wall are elongated in plane along the long axis of the ovary wall.

By the time female gametophyte is fully organized, the ovary wall becomes 9-12 layers thick (Fig. 1E, O). It shows differentiation into two zones. The outer zone comprises the epidermis and the hypodermis while inner includes the rest of the ovary wall. The cells of the hypodermis are broader than

Fig. 1. *Galinsoga parviflora.* A, B. Longitudinal sections of ovary and ovule at megaspore mother cell and organized female gametophyte stages respectively. C. Cross sections of ovary and ovule at organized female gametophyte stage. D, E. Longitudinal sections of part of ovary and ovule at megaspore mother cell and organized female gametophyte stages respectively. F. Longitudinal section of ovary and ovule at globular embryo stage. Note air space around endothelium. G. Longitudinal section of the endothelium and endosperm at heart-shaped embryo stage. H. Longitudinal section of ovary and ovule at globular embryo stage. I, J. Longitudinal section and cross section of mature fruit respectively. K. Epidermal cells of integument in surface view. L. Epidermal cells of seed coat in surface view. M. Longitudinal section of part of cotyledon showing palisade layer. N. Longitudinal section of part of mature cypsela. O. Cross section of part of ovary wall at organized female gametophyte stage. P-R. Different stages of hair development. (AS: air space, EMB: embryo, EN: endothelium, END: endosperm, ES: embryo sac, INT: integument, O: ovary, OV: ovule, OW: ovary wall, P: phytomelanin, PC: pericarp, PEZ: periendothelial zone, SC: seed coat, VS: vascular supply.)

those of the epidermis. The inner zone is again distinguishable into two regions. The region present just below the hypodermis is made up of small parenchymatous cells as seen in cross-section (Fig. 1O). This constitutes the profiber zone in the ovary wall. The inner region is composed of large parenchymatous cells.

The ovary wall is smooth in the beginning, but at the functional megaspore stage small protuberances develop from the epidermal cells (Fig. 1P). These epidermal cells become richly cytoplasmic and divide anticlinally into two daughter cells (Fig. 1Q) which elongate and divide transversely to form two long terminal cells and two short basal cells. The apical cells remain coherent by their lateral walls and elongate considerably to form a hair. Some times, the two cells of the hair part away at their tip (Fig. 1R). Hairs become thick-walled at maturity.

After fertilization, the inner zone of the ovary wall begins to separate from the outer zone. By the time embryo reaches globular stage, the hypodermal cells become glandular and start secreting phytomelanin which accumulates in between the hypodermal and profiber zones (Fig. 1H). The cells of the profiber zone also start becoming thick-walled. The phytomelanin increases in quantity, fills the schizogenous space, and soon starts depositing in between the hypodermal cells thus forming peg-like projections.

In a mature cypsela, the phytomelanin cements the two zones of the ovary wall separated earlier. The pericarp of mature cypsela is distinguishable into following zones: (a) one-layered epidermis, (b) a single layer of hypodermis, (c) phytomelanin zone, (d) fiber zone and (e) a layer of parenchymatous cells (Fig. 1N).

Fruit. Mature cypsils are black in colour and are provided with white pappus (Fig. 3A). Pappus comprises a few linear scarious fimbriate scales. Hairs are present throughout the length of the fruit. In cross-section the fruit is nearly circular in outline (Fig. 1J). It is narrow towards the base and broad on stylar side. Size of fruit is given in Tab. 1.

2) *Dahlia pinnata*. Ovary and ovule. The condition of ovary and form of ovule are similar to those described for *Galinsoga*. The vascular supply of the ovule after entering the funicle, overarches the chalaza and ends on the antiraphe side near the lower limit of the micropyle (Fig. 2A).

Integument. At the organized female gametophyte stage, the integument

is 17-20 cell-layers thick at the level of the embryo sac (Fig. 2B). However, the number varies in the other regions. The cells of the inner epidermis of the integument elongate radially and differentiate into a distinct endothelium (Fig. 2B).

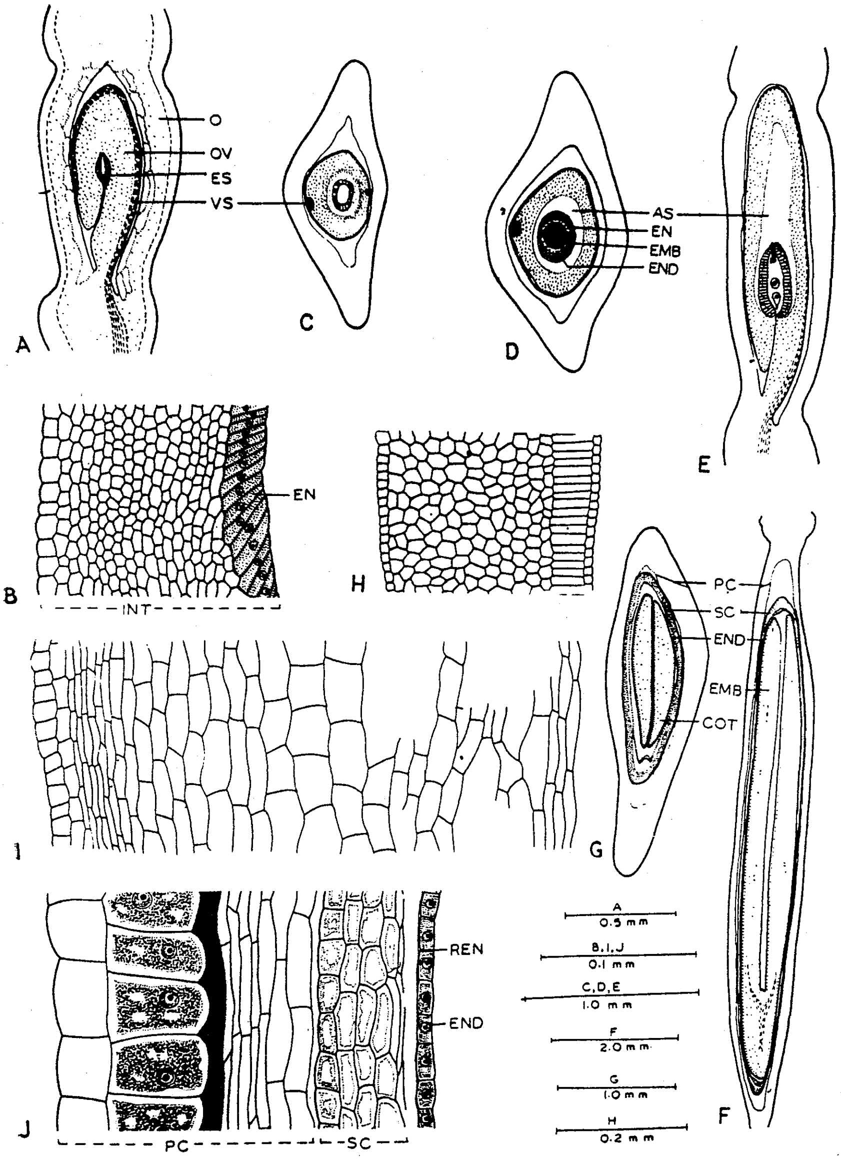
Endosperm and embryo. The endosperm is seen as a compact tissue around the globular embryo (Fig. 2D). Soon after this stage, the liquidation of the endosperm cells follows and in a mature seed only the outermost layer persists (Fig. 2J). All the cells of the endosperm show dense cytoplasm and prominent nuceli.

The mature embryo is straight and occupies the entire length of the seed (Fig. 2F). The hypodermal cells on the ventral side of the cotyledons elongate radially and form the palisade layer (Fig. 2H). Average length of embryo, hypocotyl-root-axis and cotyledons is given in Tab. 1.

Seed coat. Just after fertilization, the ovule besides endothelium shows differentiation into two zones, the outer and the inner. The former is composed of compactly arranged smaller cells having dense cytoplasmic contents and the latter is formed of large vacuolated cells constituting the periendothelial zone. In a longitudinal section, the periendothelial zone is seen extending deep into the chalazal region (Fig. 2E). The cells of the endothelium by the time divide at few places making it more than one layered (Fig. 2C, E).

By the time embryo reaches globular embryo stage, an air space appears around the endothelium (Fig. 2D). Concomitantly, the cells of the endothelium on the antiraphe side divide anti- and peri-clinally making it many layered. As the seed grows, the middle layers of the integument disorganize, and in a mature seed only 4-5 layers persist (Fig. 2J). The epidermal cells of the seed coat contain some light brown substance which gives a brownish appearance to the seed coat. No thickening of any type has been seen in the epidermal cells of the seed coat. The endothelium is represented by a thin cuticular layer in the mature seed (Fig. 2J).

Ovary wall and pericarp. The ovary is in between elliptical and rhomboidal outline at various stages of fruit development as seen in cross-sections (Fig. 2C, D, G). The ovary wall at the organized female gametophyte stage is more than 20 cell-layers thick. The epidermis and the hypodermis are single-layered (Fig. 2I) and the hypodermis is followed by strands of cells elongated in a plane along the long axis of ovary. The inner zone is composed of large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parenchymatous cells which show disorganization of its middle layers (Fig. 2A, I).

After fertilization, the hypodermis starts separating from the inner adjacent profiber zone and a schizogenous space appears between the two zones of the ovary wall. Soon, the glandular hypodermal cells start secreting phytomelanin which accumulates in the space created.

As the fruit grows, the phytomelanin gradually fills the entire space, and in a mature fruit it cements the two zones of the ovary wall separated earlier (Fig. 2J). The pericarp of mature cypsela can easily be distinguishable into following zones: (a) a layer of epidermis, (b) a layer of hypodermis whose cells are radially elongated and densely cytoplasmic, (c) a zone of phytomelanin layer which gives an undulating outline, (d) a few layers of thick-walled fiber cells, and (e) 1–2 layers of large, thin-walled parenchymatous cells (Fig. 2J).

Fruit. The mature cypsils are black in colour due to presence of phytomelanin. The fruits are oblong or obovate and compressed (Fig. 3B). The dorsal side of the fruit is more convex than the ventral side. The pappus is absent. Size of the fruit is given in Tab. 1.

Discussion In *Dahlia* (subtribe Coreopsidinae) and *Galinsoga* (subtribe Galinsoginae) the mature seed coat is composed of 3 to 4 layers of cells. In the former, cells of the seed coat do not show any ornamentation but in the latter fibrous thickenings have been observed (present study). Presence/absence of ornamentation on the cells of the mature seed coat is of considerable systematic significance. According to Robinson (1981) the Coreopsidinae seem to be characterized by firmer walled cells having straight sides and lack ornamentation but in Galinsoginae strongly ornamented seed coat have been seen. Present and our earlier observations on the seed coat of taxa belonging to subtribes Coreopsidinae and Galinsoginae (Pandey & Singh 1982, Pandey et al. 1986) also support the views of Robinson.

Fig. 2. *Dahlia pinnata*. A. Longitudinal section of ovary and ovule at organized female gametophyte stage. Note disorganization of inner region of ovary wall. B. Longitudinal section of part of integument at organized female gametophyte stage. C, D. Cross sections of ovary and ovule after fertilization and at globular embryo stages respectively. E. Longitudinal section of ovary and ovule after fertilization. F, G. Longitudinal section and cross section of mature cypsela respectively. H. Longitudinal section of part of cotyledon showing palisade layer. I. Longitudinal section of part of ovary at organized female gametophyte stage. J. Longitudinal section of part of mature cypsela. (AS: air space, COT: cotyledons, EMB: embryo, EN: endothelium, END: endosperm, ES: embryo sac, O: ovary, OV: ovule, PC: pericarp, SC: seed coat, VS: vascular supply.)

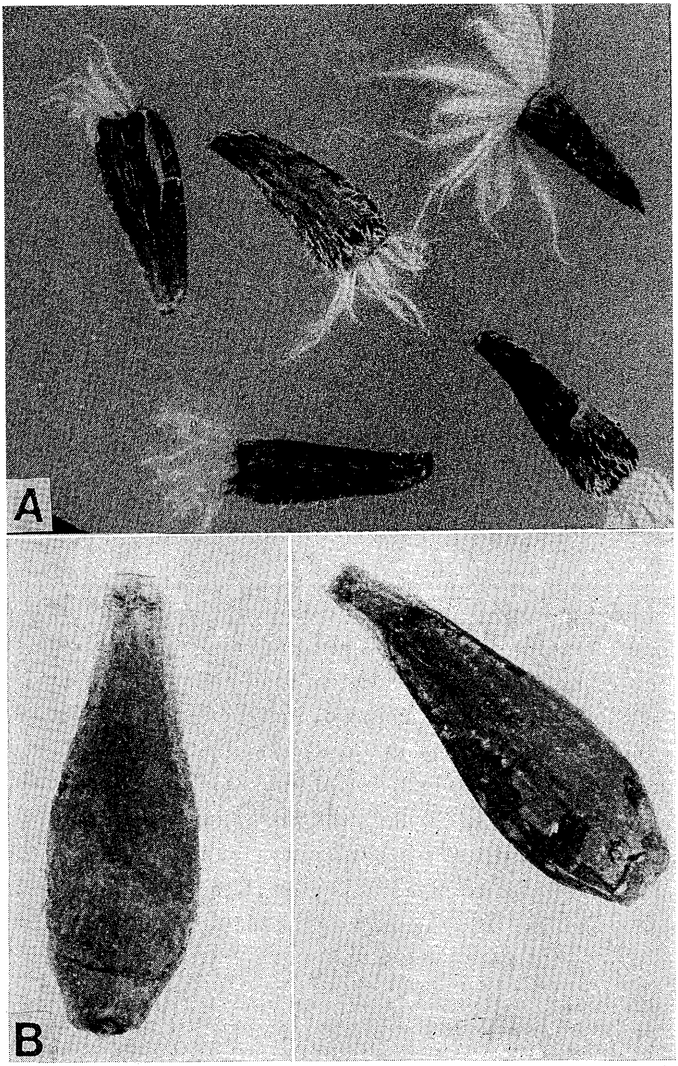

Fig. 3. A. *Galinsoga parviflora*. Mature cypsela, ×15. B. *Dahlia pinnata*. Mature cypsela, ×6.

Uniform pattern of pericarp development and differentiation is seen in both *Dahlia* and *Galinsoga*. The most significant feature of the pericarp is the presence of the phytomelanin layer which always develops between hypodermis and fiber zones. Phytomelanin layer is characteristic of all the Heliantheae (Pandey & Kumari 1987) except two subtribes, the Gaillardiinae (including the Psilotrophinae) and the Marshalliinae which lack phytomelanins in their achenes (Robinson 1981). Whether presence of phytomelanin is a primitive or derived feature is still a matter of opinion. According to Robinson (1981) if the presence of phytomelanins is a primitive feature of the Asteraceae, then their absence in Gaillardiinae, in the advanced Asteroideae including *Marshallia*, and in the subfamily Cichorioideae all represent independent losses. Recent chloroplast DNA studies (Jansen & Palmer 1987) and morphological cladistic studies (Bremer 1987) have shown that Mutisieae is the most primitive tribe in the Asteraceae and Heliantheae is derived. As phytomelanin is found only in the achenes of tribes Eupatorieae and Heliantheae and acts as a protective covering around the embryo (against desiccation, insect predation, microbial attack etc.), it is quite probable that its presence in these tribes may be a derived feature.

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aceae). Smithsonian Contributions to Botany **51**: 1-102.

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コゴメギク *Galinsoga parviflora* とダリア *Dahlia pinnata* の種子形成を研究した。共にメナモミ連に属し，前者はハキダメギク亜連 subtrib. Galinsoginae に，後者はダリア亜連 subtrib. Coreopsidinae に属する。Robinson (1981) の研究では subtrib. Coreopsidinae のものは，種子の表皮の細胞は膜が薄く特に肥厚することはないが，subtrib. Galinsoginae ものは細胞膜の一部が肥厚して模様を作るという。本研究のものも同じ結果を示した。また両種とも種皮の下皮層と繊維層との間に phytomelanin の層がある。これは今まで原始的な群にみられる性質と考えられていたが，最近の研究では逆に進化した性質と考えられるようになった。

□木原　均・篠遠喜人・磯野直秀(編)：**近代日本生物学者小伝** 567 pp. 1989. 平河出版社，東京. ¥4,500. 74名の執筆者(故人13名)が1名ずつの著名な生物学者の小伝(各3-6頁)を担当したもの。主として「採集と飼育」「遺伝」に発表されたものを再編しているが，書き下ろし15篇もある。これらの「小伝篇」のほかに，頭初に木村陽二郎(2篇)，上野益三，内田亨(各1篇)の明治・大正通史（国立科学博物館，1977）の「通史篇」がある。専門分野の異なる先覚者の一生には，初めて知って驚くような記事もあり，啓発されることが多かった。本書の編集・レイアウトは極めてスマートで，小伝に採り上げられた生物学者の小型の肖像写真・小年譜とともに自然に記事に誘いこまれる。篠遠は「まえがき」で，正伝ではなく，あくまでも小伝であると特にことわっている。磯野は先駆者および後継者たちの事蹟が個々には不分明のことが多いのを嘆いて，本書を編したという。小伝の著者たちの記述の仕方はさまざまであるが，本書によって日本の生物学の流れの大筋を汲みとられたいという。できれば年表を付けて，全体の統一を図りたかったともいう。しかし，篠遠の多年にわたる意図はほぼ達成されたかに見える。本書を入手した夜は興に引かれて，読書は深更に及んだ。　（津山　尚）

□矢野　亮：**街の自然観察** 200 pp. 1989. 筑摩書房，東京. ¥950. べつにわざわざ山や海に行かないでも，すぐ身近なところで自然を見つけたり遊んだりすることができるということを，たくさんの事例で示したもの。国立科学博物館自然教育園勤務の著者だけあって，動植物のいろいろな見方が紹介されている。　(金井弘夫)